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THE EMBRYO SAC OF EPIPACTIS[1]

WILLIAM H. BROWN AND LESTER W. SHARP

(WITH PLATE X)

The present study is based upon material of *Epipactis pubescens* (Willd.) A. A. Eaton, collected at Cold Spring Harbor, N.Y., in August 1909.

The archesporium is distinguishable very early as a single hypodermal cell which terminates an axial row surrounded by a single epidermal layer. As growth proceeds, the young ovule becomes strongly anatropous and develops two integuments, the outer one being continuous with the slender stalk. Since the normal heterotypic prophases always occur in the nucleus of the archesporial cell preparatory to its first division, it is to be regarded as the megaspore mother cell, no parietals being formed.

The subsequent course of development to the complete embryo sac is not identical in all ovules, the same end being reached by a variety of methods. The behavior in what probably represent the majority of cases is as follows. After becoming considerably enlarged, the megaspore mother cell undergoes its first division (fig. 1). Since the spindle lies near the micropylar end of the mother cell, the resulting daughter cells are very unequal in size (fig. 2). The larger, chalazal cell again divides unequally, forming two megaspores, while in only a single case was the micropylar daughter cell observed in process of division (figs. 3 and 4). The innermost megaspore enlarges and gives rise to the embryo sac, while the other cells of the row soon degenerate.

The nucleus of the functioning megaspore divides to two (fig. 5), and very soon small vacuoles appear in the cytoplasm, mostly in the region between the two nuclei. Meanwhile the sac grows considerably, but continues to have the general shape of the megaspore mother cell. As growth proceeds, the increase in volume of the cytoplasm fails to keep pace with that of the sac cavity, so that the small vacuoles in the central region coalesce to form a large central one (fig. 6), the cytoplasm becoming spread out as a parietal layer which is thickest at the ends of the sac where the radius of curvature is small. The two nuclei lie in these two regions. These nuclei soon divide simultaneously, giving rise to the four-nucleate sac (fig. 7). In this division and in the preceding one no traces of cell plates could be distinguished on the spindle fibers. After considerable enlargement of the embryo sac, the third division occurs, the two spindles formed in each end varying in position. Usually they lie approximately at right angles to each other; in such cases they may be equidistant from the end of the sac (fig. 8), or one may lie at a little distance from the other along the lateral wall. Cell plates appear on the fibers of all four spindles, so that the resulting eight nuclei are separated in the usual manner. In the micropylar end the transverse spindle gives rise to the two synergids, while the longitudinal one forms the egg and polar nucleus. In the chalazal end three antipodal cells and a polar nucleus are formed in an exactly similar manner (fig. 9). The egg and synergids increase in size, and the two polar nuclei approach each other and fuse (fig. 10).

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[1] Contribution from the Botanical Laboratory of the Johns Hopkins University No. 19. The account of the development of the embryo sac was written by Mr. SHARP, and the discussion by Mr. BROWN.

Exceptionally the two spindles in the chalazal end of the sac, instead of lying at right angles, come to lie more or less parallel to each other and usually to the longitudinal axis of the sac (fig. 11). As division proceeds they may become coalesced, forming one large spindle instead of two ordinary ones (figs. 12–14). The conclusion that such is the explanation of the large spindle shown in fig. 12 is supported by the fact that the plate of chromosomes could be seen by focusing to be made up of two groups of approximately equal size, and that altogether their number was plainly larger than that in either of the micropylar spindles. The same was true of the corresponding spindle of fig. 13. The division of this double spindle may keep pace with that of the micropylar ones (fig. 12), or it may be delayed as shown by figs. 13 and 14. In fig. 14 the wall on the fibers of the chalazal spindle is only slightly younger than those of the micropylar ones, showing but a slight delay. In fig. 13 the delay has been greater, the chromosomes of the chalazal spindle having very recently separated, while in the micropylar end distinct walls and nuclear membranes are present. The wall which appears on the fibers of the double spindle cuts off one nucleus in the base of the sac, and leaves one free in the cytoplasm (fig. 15). In these cases the latter nucleus apparently fuses with the polar nucleus from the typical micropylar group, while the one cut off by the wall later disorganizes (fig. 16). That such a six-nucleate condition offers no hindrance to fertilization is evidenced by the sac represented in fig. 16, in which a two-celled embryo is present.

In fig. 11 the chalazal spindles have taken up a nearly parallel position, but at too late a stage to coalesce, since membranes are already present about the four nuclei. It is probable that in this case a continuous wall would be formed across the base of the sac, cutting off two nuclei and leaving two free in the cytoplasm, but no sac was observed in which such an end had been reached. These phenomena appear in most cases to be in some way associated with a narrow configuration of the chalazal end of the sac at this time, and a consequent diminution in the amount of cytoplasm present there.

In other cases the fate of the megaspore mother cell is quite different from that described in the foregoing account. After enlarging somewhat the nucleus divides, the spindle lying at about the center of the cell, so that the thin wall formed upon the fibers separates the mother cell into two nearly equal daughter cells (fig. 17). The wall, however, soon disappears, leaving the two nuclei in a single cell cavity which is to form the embryo sac. Between the nuclei vacuolation occurs, so that the center of the sac comes to be occupied by a single large vacuole, the two nuclei taking up positions at opposite ends of the sac, where the greater part of the cytoplasm lies (fig. 18). Aside from the conspicuously larger size of the sac and its nuclei, this stage is closely similar to the corresponding one of a sac derived from a single megaspore. It is important to note that here the epidermal layer of the nucellus could be seen to be everywhere in contact with the sac, degenerating cells being clearly absent (cf. figs. 6 and 18).

The two nuclei again divide, and delicate walls appear on the spindle fibers between each pair of resulting nuclei. Later both walls may become quite distinct (fig. 19), though they vary somewhat in position owing to the various planes in which the spindles may lie. In the figure shown they are transverse to the longitudinal axis of the sac, so that the four nuclei have a linear arrangement. Usually, though not always, these walls disappear very soon. In the event of their complete disappearance, there results a four-nucleate sac like that represented in fig. 20, which is essentially the same as one derived from a single megaspore, but is conspicuously larger. That the four nuclei here shown have resulted from fewer divisions from the nucleus of the archesporial cell than have those in four-nucleate sacs derived from one megaspore seems to be indicated by their relatively larger size (cf. figs. 7 and 20). A similar condition was pointed out in connection with the two-nucleate stage (cf. figs. 6 and 18).

At a stage as late as the four-nucleate sac it becomes very difficult to determine whether degenerating cells at the micropylar end of the sac are present or not, so that it is unsafe to depend too strongly upon them as a criterion, but after the examination of a large number of cases the present writers hold the view that the four nuclei, which, on account of their origin and the appearance of walls at the mitoses which give rise to them, are megaspore nuclei, and that these by one further division give rise to an eight-nucleate sac entirely similar to one derived from a single megaspore.

Important evidence in this connection is afforded by the wall formed between the two chalazal (megaspore) nuclei, which often shows a tendency to persist. In fig. 21 it is still visible as a remnant during the division to form the eight nuclei of the sac, the four spindles in this case showing an unusual irregularity in distribution. Since one of the micropylar spindles was in an adjacent section, it was not possible to demonstrate the presence of a wall in that end. In other cases the wall persists for a longer time, giving rise to the condition shown in fig. 22. Here it is observed separating the two undivided chalazal nuclei, while at the micropylar end the next division has taken place, cell plates being evident on the spindle fibers. A somewhat later stage is represented in fig. 23. The persistence of the wall seems to result in a delay of the nuclear divisions (fig. 21), or in their suppression, as shown by figs. 22 and 23.

The fact that in these cases the wall between the two chalazal nuclei is decidedly thicker than those between the micropylar nuclei would seem to indicate that it had been formed at the time of megaspore formation rather than later by a double spindle as described above, for in the latter case the division of the double spindle lags behind that of the micropylar ones. It thus appears that a six-nucleate sac of this type may originate by either of two methods.

Should the wall formed at the first division of the megaspore mother cell persist until after the second division, we should have a development similar to that of *Smilacina* (McALLISTER 9), in which the walls separating the four megaspores break down, leaving in a single large cell the four nuclei, which then divide once to form an eight-nucleate sac.

A number of two-nucleate sacs were observed with apparently but one degenerating cell present at the micropylar end. Further evidence on this point was not obtained, but these may represent cases in which the embryo sac is being derived from a daughter cell, or, in the light of the above, from two megaspores.

The development of embryo sacs from two or from four megaspores in a plant, which also forms them from one megaspore in the usual manner, may be regarded as steps in the reduction of the number of nuclear divisions occurring between the archesporial cell and the formation of the egg. When four megaspores take part in the formation of an eight-nucleate sac, the egg is removed from the archesporial cell by three divisions, as is also the case in *Cypripedium* (PACE 11), in which the egg nucleus is one of four formed in one daughter cell. Should one more division in any way be eliminated, the egg nucleus then being one of the four products of the reducing divisions, the gametophytic generation would be represented by a single nucleus, and the condition would be exactly comparable to that of the animal egg.

The further fate of the embryo sac, whether derived from one, two, or four megaspores, is apparently the same. The pollen tube makes its way through the micropyle into the sac, disorganizing one of the synergids, and liberates two male nuclei, one of which fuses with that of the egg, and the other with the product of the fusion of the polar nuclei (fig. 24). The endosperm nucleus which results from this fusion enlarges but does not divide, and soon degenerates along with the antipodals (fig. 25).

The first division of the fertilized egg is transverse (fig. 16). The second division is in the micropylar cell and is also transverse, while the third (fig. 25) separates the chalazal cell into two by a longitudinal wall. These two divisions frequently occur simultaneously. Intermediate stages in the development of the embryo were not observed, but in the mature seed, which is of the usual orchidaceous type, it consists of a small, oval, undifferentiated mass of cells with no suspensor.

Discussion

Owing to the definite course of development in many of the animal eggs, the zoologists have been able to study some of the factors concerned. They have found in some cases that structures develop independently. In others some organs do not appear if certain parts are wanting, while in still other cases, as the lens of the amphibian eye (SPEMANN **14**), structures, which at one time probably required the presence of another organ for their development, have during the course of evolution come to develop independently.

The factors concerned in the development of plants have been studied much less than in the case of animals. This is perhaps due to the fact that most of the plants which show determinate development are inclosed, during their early stages, in the tissues of the parent. It is well known, however, that the form of a plant may be greatly affected by external conditions. A striking case is that of *Stigeoclonium*, in which, according to LIVINGSTON (**8**), the cells develop into a palmella stage or elongated filaments according to the osmotic strength of the nutrient solution. HARPER (**6**) in studying *Hydrodictyon* concluded that the shape of the net was due to the shape of the parent cell, while the axis of elongation of the individual cells was connected with the pressure exerted by neighboring cells upon each other.

In *Epipactis* it is not evident why the nucleus of a megaspore should in some cases develop into the nuclei of a whole embryo sac, and in others into those of only a portion of one. This may be due, however, to some condition such as nutrition, which is external to the megaspores, and is probably not due to potentialities inherent in the various megaspore nuclei, for it would seem that the nucleus of each megaspore, if placed under proper conditions, would have the potentialities for producing the nuclei of a complete sac. This conclusion is supported by the large number of cases in which the development of more than one megaspore in a tetrad has been described (COULTER and CHAMBERLAIN **4**). Differences in the potentialities of the megaspore nuclei, moreover, could not explain the differences in development, for the course can be predicted at metaphase of the reducing division. Different potentialities if they existed would, therefore, have to be in the nuclei of the different megaspore mother cells; but according to present theories of heredity all mother-cell nuclei possess equal potentialities. The most reasonable conclusion would seem to be that the different courses of development are due to conditions external to the nuclei, and that the fate of a nucleus will depend on its position. It would seem probable, moreover, that the conditions which determine the fate of a nucleus, when four megaspores combine to form a normal sac, must be the same as those which determine the fate of the nuclei of a sac formed from a single megaspore. The formation of a normal sac from four megaspores in *Lilium* (COULTER and CHAMBERLAIN **4**), *Smilacina* (MCALLISTER **9**), and also in the large number of cases in which a row of megaspores is not formed, as well as from the aposporous outgrowths into the cavity of the degenerated embryo sac of *Hieracium* (ROSENBERG **13**), and in *Alchemilla* (MURBECK **10**) from the megaspore mother cell without a reduction in the number of chromosomes, would seem to indicate that the formation of a sac is not due to the nature of the cell from which it is produced, but that a normal sac will be formed from any cell subjected to the conditions under which a megaspore would produce one. The determining conditions in all of these cases, or at least most of them, are probably the same as in *Epipactis*, and since these conditions appear to be widely distributed among the angiosperms, they may have been the original cause of the evolution of the eight-nucleate sac. This could be true even if it should be shown that some normal sacs are formed without the original determining condition, for cases apparently quite similar to this are known among animals. A striking example is the lens of the amphibian eye (SPEMANN 14), which in some species requires the presence of the optic cup for its development, while in others it develops even if the optic cup is removed.

From the foregoing discussion it does not follow that the nuclei play a passive part in development; for the external conditions which influence them may in turn be due to the nuclei from which these have been derived, i.e., the vegetative nuclei of the plant; and if a nucleus were other than it is, it probably could not react to external conditions to produce the structures which it does.

Any analysis of the conditions determining the course of development of the embryo sac must at present be incomplete and largely tentative, but a comparison of the conditions under which various types of sacs are formed may be worth while, as it is likely to suggest new ways of looking at their origin and development. The first point to be considered is the production of polarity. Before the megaspore mother cell divides, it has the general shape of the mature sac, and an enlargement of the whole nucellus without further change would preserve this shape. The formation of the megaspores in rows in most angiosperms, and the elongation of the nucellar cells in a direction parallel to this row would indicate that the elongated shape of the functional megaspore and the sac is connected with the direction of greatest pressure in the nucellus. When the nucleus of the mother cell divides, the daughter nuclei, as is usually the case, tend to be evenly distributed in the cytoplasm. After vacuolization, a continuation of this same tendency would carry the nuclei to the two ends of the sac, where surface tension would cause the accumulation of the cytoplasm. The conclusion that this is the explanation of polarity is supported by the development of the sixteen-nucleate sacs. In *Peperomia sintenesii* (BROWN 1), where the sac would seem to be derived from four megaspores, the mother cell and embryo sac are both rounded, and there is no polarity. The same thing is true in the Penaeaceae, where Miss STEPHENS (15) believes that the embryo sac is derived from four megaspores. In *Peperomia hispidula* (JOHNSON **7**) and in *Gunnera* (ERNST **5**) the embryo sac is rounded at the four-nucleate stage and there is no polarity, but as development proceeds the sac elongates and polarity is produced. In *Strelitzia* (BROWN **3**) there are four megaspores, each of which may germinate, but the three micropylar ones degenerate and the sac is always formed from the chalazal one. The three micropylar megaspores are not elongated and their nuclei do not show a polar arrangement.

At the second division of the embryo sac of *Epipactis* the spindles are arranged so that the daughter nuclei are again evenly distributed in the cytoplasm.

At the third division the spindles in both ends are usually arranged approximately at right angles to each other. This is of course usually the case in the ends of embryo sacs and in other rounded masses of cytoplasm, and would seem to be the way in which the spindles and resulting nuclei would be most evenly distributed. In *Epipactis*, however, the chalazal end is sometimes narrow, and in this case the two spindles lie side by side. The simultaneous division of the nuclei and the production of an equal number in each end is probably connected with the similar conditions in the two ends. The number of nuclei is very likely due to some kern-plasma relation. In later stages the similarity of the two ends is destroyed and the nuclei take on quite different appearances. In *Epipactis* there is sometimes less cytoplasm in the chalazal than in the micropylar end, and this is connected with a delay in the divisions in the chalazal end.

STRASBURGER (**16**) has pointed out that the walls produced at the last division in a normal eight-nucleate sac are formed on the fibers connecting the nuclei, and that since one nucleus at each end is nearer the center than the other three, no wall is formed around it, thus leaving it free in the cytoplasm. He ascribes the fusion of these two polar nuclei to the fact that they have ceased developing and are in the same cell cavity. Evidence strengthening this position has been constantly accumulating and, as previously pointed out (BROWN **1**), is quite striking in the case of the sixteen-nucleate sacs, where all of the nuclei not cut off by walls fuse to form the endosperm nucleus. In *Epipactis* the polar nuclei are produced in a variety of ways, but always fuse to form the endosperm nucleus, although this does not develop further.

It would seem that even the final fate of the nuclei may depend largely on interacting conditions, for the synergids in those cases in which a sac is formed from four megaspores, as in the normal cases, are formed from the pair of nuclei arising from the transverse spindle. That the nuclei at this stage are equipotential is indicated by the occasional fertilization of one of the synergids (COULTER and CHAMBERLAIN 4). The structure of eggs, synergids, antipodals, etc., probably depends largely on the nature of the protoplasm of which they are constituted, and is of course widely different in different plants; but the part which any particular nucleus in *Epipactis*, and probably in other angiosperms, is to produce, as well as the general arrangement of the sac, apparently depends on the relation of the nucleus to other parts rather than upon any quality inherent in it.

According to the above interpretation, the embryo sac in its early stages may be regarded as a system, all parts of which are equipotential, the fate of the different parts being connected with conditions external to them. The course of development in certain animal eggs is connected very largely with a stratification of the materials composing them, but in the early stages of many of these eggs a cell may develop into a whole embryo or some fraction of one, depending on whether or not it is separated from others. This dependence of the course of development of a cell on its relation to conditions external to it, therefore, seems to be common to both plants and animals.

The foregoing analysis, in so far as it goes, may be taken as indicating that the parts concerned act according to mechanical principles and do not need a vitalistic force to explain their behavior. This would seem to be true of any analysis which shows an orderly relation between an antecedent and consequent event, because for a thing to be mechanistic (this term being used in its widest sense) means simply that when the events are reduced to their simplest terms they take place in an orderly and predictable sequence. An analysis may bring to light new elemental laws of a different kind from any that we know at present, but in so far as they are laws of an orderly sequence, they will be as good a mechanical explanation as any other law, for a law can only state the sequence, and it is outside the realm of science to explain why one event follows another. Any vitalistic explanation must therefore be either outside and supplementary to science or contrary to the fundamental postulate of all science, namely, that the same antecedent conditions are always followed by the same consequent ones.

If we compare the development of the angiosperm embryo sac with that of the gymnosperms, we find in the early stages a striking similarity between those of the gymnosperms and the sixteen-nucleate sacs of the angiosperms. In both cases the nuclei are fairly numerous, evenly distributed in the cytoplasm, and do not show a polar arrangement. This similarity, however, is probably derived and not primitive in the case of the sixteen-nucleate sacs, for some of these, at least, are derived from four megaspores. There would appear to be in the gymnosperm embryo sac nothing similar to the striking polarity shown by those of most angiosperms, but that the same factors are at work is perhaps indicated by the elongated shape of the embryo sacs of many of the gymnosperms, as well as the tendency toward a reduction in the number of nuclei, and the presence of a large central vacuole. Likewise the presence in the early stages of the gymnosperm embryo sac of free nuclei surrounded by a cellular region may foreshadow the free polar nuclei of the angiosperms. PORSCH (**12**), in an excellent discussion of the phylogeny of the angiosperm embryo sac, has attempted to point out a similarity between the archegonia of the gymnosperms and the two polar groups in the angiosperms. When we remember, however, that in those gymnosperms which have archegonia they are initiated in a cellular phase and the polar groups of the angiosperms in a non-cellular one, it would seem that any similarity between the development, final structure, or factors concerned must be rather superficial. It would probably be better to regard the structure of the angiosperm embryo sac as the result of new physiological conditions which have arisen in connection with the reduction of its size and the number of its nuclei.

Summary

1. The archesporium of *Epipactis* consists of a single hypodermal cell, which, without formation of parietals, functions as the megaspore mother cell.

2. In most cases the megaspore mother cell divides to two unequal daughter cells, the chalazal one again dividing to form two megaspores. The innermost megaspore then gives rise to the embryo sac.

3. In other cases four megaspores take part in the formation of the sac, the walls appearing at the first two divisions of the megaspore mother cell being evanescent. At least one of these walls often shows a tendency to persist, which results in a six-nucleate type of sac. The same appearance may also result from irregularities in the orientation of spindles.

4. There is some evidence that the embryo sac may at times be derived from two megaspores.

5. The normal mature embryo sac contains an egg, two synergids, three evanescent antipodal cells, and two polar nuclei which fuse.

6. The usual type of "double fertilization" occurs.

7. The fertilized egg gives rise to an embryo, which, at least in the seed, has no suspensor.

8. The endosperm nucleus, formed by the fusion of one male nucleus with the two polar nuclei, disorganizes without dividing.

9. The variety of methods by which the embryo sac of *Epipactis* is formed may be regarded as a series representing a reduction in the number of nuclear divisions occurring between the archesporial cell and the formation of the egg.

10. The fate of the nuclei in the different courses of development is probably due to some conditions external to them rather than to any inherent potentialities. A normal sac would probably be produced by any cell subjected to the conditions under which a mother cell would produce one.

11. The sac in its early stages appears to be an equipotential system, polarity being connected with its shape, and the part that the nuclei are to play with their position.

12. The polar groups probably do not represent archegonia,

but the general structure of the angiosperm embryo sac may be indicated by some features in those of the gymnosperms.

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EXPLANATION OF PLATE X

All figures were drawn with the aid of an Abbé camera lucida, and show a magnification of 900 diameters. The following abbreviations are used: *a*, antipodals; *d*, daughter cell of megaspore mother cell; *e*, endosperm nucleus; *m*, megaspore; *pt*, pollen tube; *s*, synergid; ♂, male nucleus.

FIG. 1.—First division in the megaspore mother cell.

FIG. 2.—Daughter cells resulting from division of megaspore mother cell.

FIG. 3.—Two megaspores formed by the division of the chalazal daughter cell, and the undivided micropylar daughter cell.

FIG. 4.—Micropylar daughter cell dividing; the only case observed.

FIG. 5.—Young two-nucleate sac; spindle fibers still present; no separating wall; abortive megaspore and daughter cell represented by two deeply staining masses.

FIG. 6.—Two-nucleate sac after formation of central vacuole.

FIG. 7.—Four-nucleate sac.

FIG. 8.—Division to form eight nuclei.

FIG. 9.—Eight-nucleate sac.

FIG. 10.—Fusion of polar nuclei.

FIG. 11.—Division to form eight nuclei; the two chalazal spindles show a tendency to become parallel to each other.

FIG. 12.—Metaphase of a similar division; the two chalazal spindles have coalesced to form a single large spindle.

FIG. 13.—Later stage; the division of the coalesced chalazal spindles lagging behind that of the micropylar ones.

FIG. 14.—Telophase of a similar division; wall appearing on the fibers of the spindle formed by coalescence.

FIG. 15.—Wall complete; the nucleus cut off in the base of the sac beginning to disorganize; its sister nucleus free in the cytoplasm with the polar nucleus of the micropylar group.

FIG. 16.—Sac containing two-celled proembryo, endosperm nucleus, disorganized cell in base, and pollen tube.

FIG. 17.—Nearly equal division of megaspore mother cell; wall formed on the spindle fibers.

FIG. 18.—Later stage; the wall has disappeared and a central vacuole has formed.

FIG. 19.—Four megaspore nuclei with evanescent walls.

FIG. 20.—Four megaspore nuclei; the walls have disappeared.

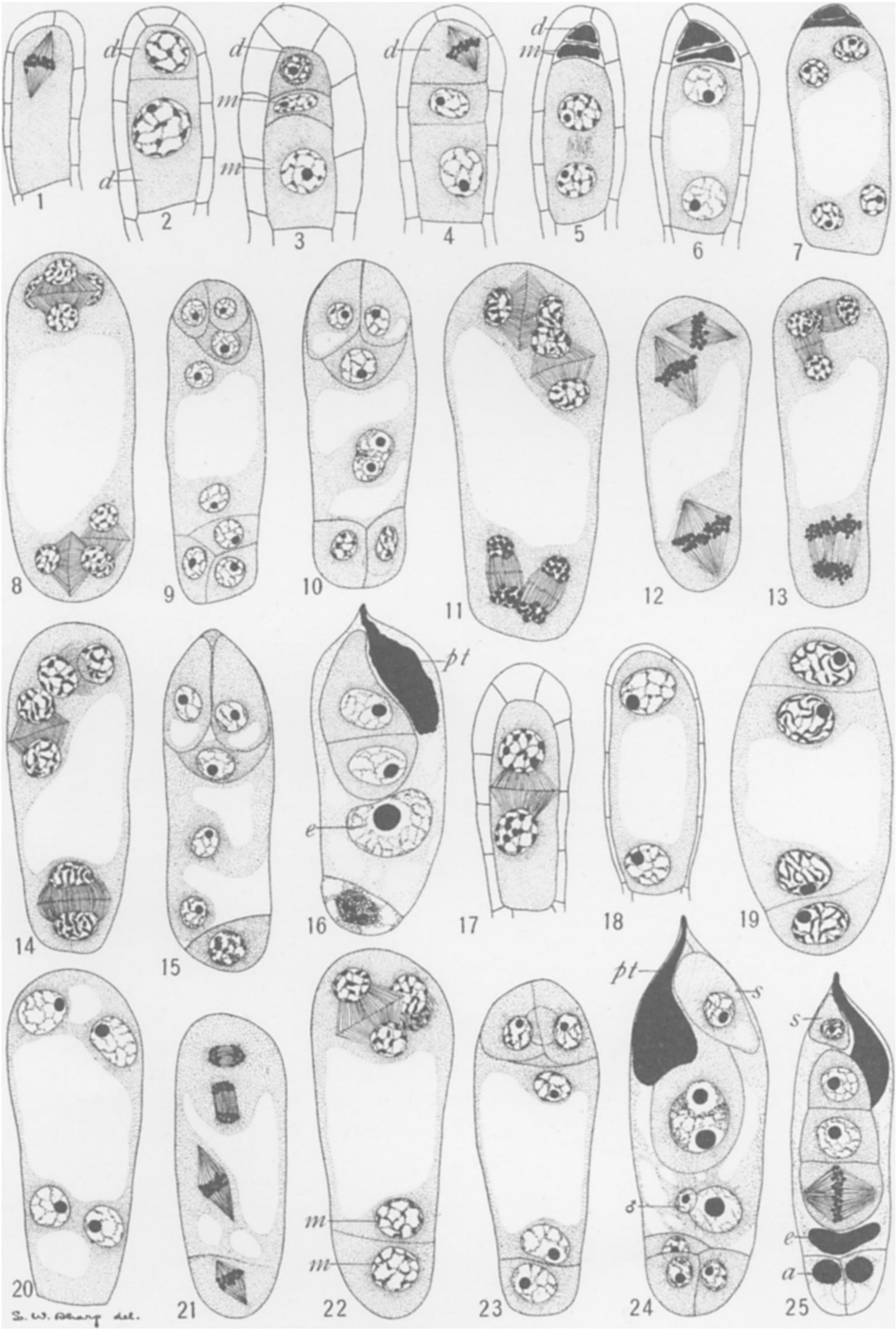
FIG. 21.—Four megaspore nuclei dividing to form the eight nuclei of the sac; megaspore wall still evident in chalazal end.

FIG. 22.—Sac in which the chalazal megaspore wall has persisted.

FIG. 23.—Later stage; walls in micropylar end complete.

FIG. 24.—Double fertilization in a typical eight-nucleate sac.

FIG. 25.—Sac containing young embryo; endosperm and antipodal nuclei disorganizing.



BROWN and SHARP on EPIPACTIS